

Review of the muricine subgenus *Pterynotus* (*Pterochelus*) in Australia

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ABSTRACT

Four species of the muricine subgenus *Pterochelus* are distributed around the perimeter of the Australian continent in a simple geographic pattern: *P. acanthopterus* in the north; *P. duffusi* in the east; *P. triformis* in the south; and *P. westralis* in the west. To this number may be added two geographically intermediate species: *Pterynotus* (*Pterochelus*) *akation*, n. sp., in the northwest; and *P. (P.) undosus*, n. sp., in the southwest. The species *P. saibaiensis* was named from the northeast, but it is here considered to be a synonym of *P. acanthopterus*, which thus ranges from the Torres Strait to Rottneest Island, W.A.

INTRODUCTION

Three species of the muricine subgenus *Pterochelus* (type species: *Murex acanthopterus* Lamarck, 1816) have been recognized as occurring in Australia — *P. (P.) acanthopterus* in the north and west, *P. (P.) triformis* (Reeve, 1845) in the south and *P. (P.) duffusi* (Iredale, 1936) in the east. A fourth species, *Pterynotus westralis* Ponder and Wilson, 1973, was described in the subgenus *Pterochelus* but, at the same time, the authors expressed reservations concerning the validity of the subgeneric taxon (Ponder and Wilson, 1973, p. 395).

Closer examination of many specimens from around the perimeter of the Australian continent shows that there are at least two additional species, the so-called "dwarf-form" of *P. acanthopterus* (e.g., Radwin and D'Attilio, 1976, p. 96) from the northwestern corner (pl. 5, figs. 1-5) and another previously unrecognized species from the southwest (pl. 6, figs. 1-4).

In addition to the array of species found in Australian waters, there is possibly one other living species of *Pterochelus*. This is *P. (P.) ariomus* (Clench and Pérez Farfante, 1945) based upon a unique specimen (pl. 3, fig. 8) taken live off Hollywood, Florida. In a previous study of this group (Vokes, 1989), I discussed my reasons for accepting this species. Even though there has never been another specimen taken, the presence of a closely related form in the Pliocene of England (*Murex elegantula* Harmer, 1918) together with a long fossil record going back to the Eocene in England (*Murex bispinosus* Sowerby, 1823) and the Oligocene of the United States and Germany (*Murex angelus* Aldrich, 1886), indicates to me there is a strong possibility that this is a valid western Atlantic species. Certainly, it is not recognizable as any known form from Australia. With its relatively small size and coarse ornamentation the species it most nearly resembles is *P. elegantula*.

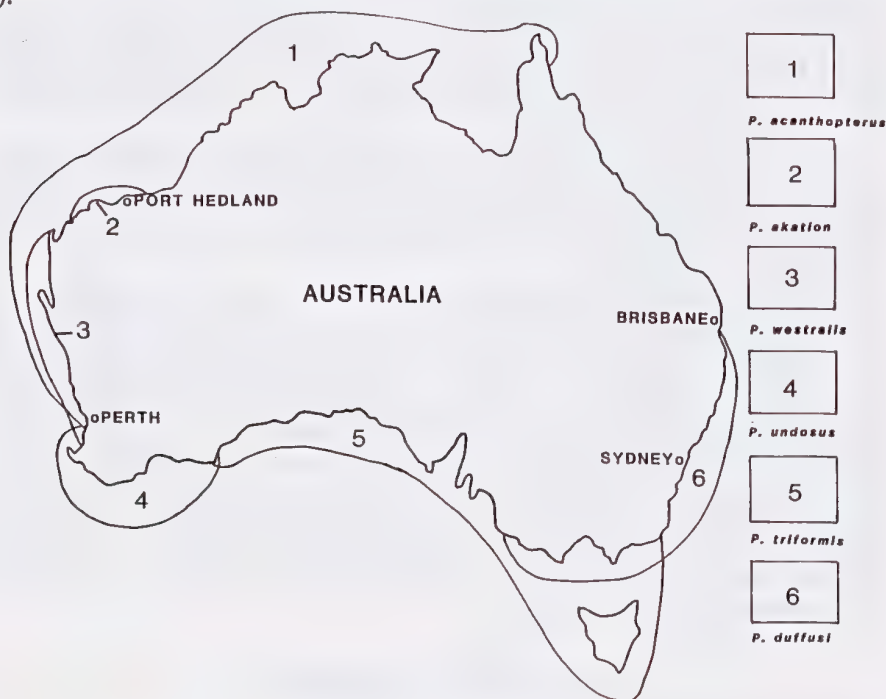
MATERIALS AND METHODS

This study is the result of two trips to Australia, one in May, 1992, and one in

December, 1992-January, 1993. At that time I examined not only all of the relevant material in the collections of the Australian Museum and the Western Australian Museum, but also every private collection that I could locate, including several public/private museums of the sort commonly found in Australia. In addition, in the thirty years that I have been studying the species of Muricidae I also have studied the collections at the National Museum of Victoria, the South Australian Museum, and the British Museum (Natural History), as well as numerous private collections in the United States.

Until truly quantitative methods utilizing genetic material (*e.g.*, radio-immuno-assay) become better developed (and I believe in time this will happen) the *only* way that species of Mollusca are separated is in the eye of the beholder. One must examine as many specimens as possible and hope that a consistent pattern of morphologic characters can be recognized. This method is almost totally subjective. There are certain morphological characters, such as the protoconch or the operculum, that sometimes prove to be useful in separating superficially similar species. But, ultimately, it is the practiced eye of the taxonomist that makes the value judgement as to whether two shells are sufficiently different to be considered two distinct species.

The muricid radula is an extremely valuable tool in separating taxa at the subfamilial and occasionally even at the generic level. However, at the species level it is useless. Therefore, the single SEM photograph of the radula of *Pterynotus (Pterochelus) undosus*, n. sp. (text-figure 3) can serve for all of the species discussed herein. Moreover, the radulae of three of the previously described species have been figured elsewhere: *P. acanthopterus* (Ponder, 1972a, text-figs. 1:2a, 2b); *P. duffusi* (Radwin and D'Attilio, 1976, text-fig. 61); *P. westralis* (Ponder and Wilson, 1973, text-figs. 1, 2).



Map showing geographic distribution of the species of *Pterochelus* in Australia.

Between some species of Muricinae different protoconch types, reflecting differing reproductive strategies, facilitate distinction. However, in the subgenus *Pterochelus* protoconchs of all of the species are identical, consisting of one and one-half bulbous whorls, implying direct development. The only difference between the various species may be seen in the diameters of certain of the forms. For example, specimens of *P. (P.) duffusi* have a relatively large protoconch with a diameter of approximately 1.5 mm (varying from 1.3 mm to 1.6 mm) in contrast to specimens of *P. (P.) undosus*, n. sp., which has a protoconch of approximately 1.0 mm diameter (varying from 0.9 to 1.1 mm). This can be seen visually by comparing pl. 4, fig. 1c (*P. duffusi*) and pl. 6, fig. 3d (*P. undosus*).

In all of the measurements given below, "length" is that distance from the apex of the shell to the distal end of the siphonal canal, measured perpendicular to the axis of the shell. "Width" is the distance from the outermost edge of the varical lip (including any shoulder spine that may be present) to the opposite side on the shell, as measured on a line *through*, and parallel to, the axis of the shell. Thus, on these three-variced species, this point is usually the intervarical node between the second and third varices, counting abaperturally.

SYSTEMATIC DESCRIPTIONS

Genus *Pterynotus* Swainson, 1833

Pterynotus Swainson, 1833, Zool. Illus., (Ser. 2) v. 3, expl. to pl. 100.

Type species: *Murex pinnatus* Swainson, 1822, by subsequent designation, Swainson, 1833 [*ibid.*, expl. to pl. 122].

Subgenus *Pterochelus* Jousseau, 1880

Pterochelus Jousseau, 1880, Le Naturaliste, Année 2, p. 335.

Type species: *Murex acanthopterus* Lamarck, 1816, by original designation.

Discussion: Ponder and Wilson (1973, p. 395), in their description of *P. westralis*, discussed the probability that the subgenus *Pterochelus* is "not worthy of recognition even as a subgenus." If *P. westralis* were the only species to be referred to the group this would be a fair assessment. But other members of the subgenus have a distinctive morphology, which has existed since the Eocene in an almost unchanged form. Even though *P. westralis* is minimally distinct from the nominal genus, the other species of the group are certainly worthy of separation.

The problem arises because *P. (P.) westralis* is intermediate between typical *Pterynotus* s.s. and the subgenus *Pterochelus*, which is marked by having the aperture opening into a channel in the shoulder spine, extending to the edge of the varix. It is only this latter trait that separates the two taxa, other criteria such as scabrousness, nature of protoconch, and radular type are too similar (or have broad, overlapping ranges in each of the subgenera) to distinguish the two. Nevertheless, the *Pterochelus* morphotype goes back to the Eocene of England (*Murex bispinosus* Sowerby, 1823) and Australia (*Murex adelaidensis* and *manubriatus*, both Tate, 1888*) almost without change. For a trait to persist so long through geologic time in an unchanged fashion suggests there is a strong evolutionary reason for its presence.

* The species *Murex otwayensis* Harris, 1897, originally thought to be Eocene is now known to be from the Oligocene Glen Aire Clay. It is not a *Pterochelus*, but a *Pterynotus* of the "species group of *P. guesiti*" (see below), very similar to the American Eocene *P. stenzeli* Vokes, 1970, with a denticulate outer lip and only a slight infolding of the apertural margin into the channeled shoulder spine.

Ponder (1972a, p. 216) originally suggested that the genus *Pterynotus* s.s. be retained for those species without a posterior spine, with scabrous sculpture and a multispiral protoconch. However, as Ponder and Wilson noted (1973, p. 395), *P. westralis* has shell characteristics of both. Even more importantly, if the multispiral protoconch were made a generic character, most of the species presently included in the strict subgenus would be eliminated. It is now well established that the nature of the protoconch, whether multi- or paucispiral, although a good specific character, is not a valid generic character (e.g., Ponder, 1972b; Ponder and Vokes, 1988).

In the Recent fauna the subgenus *Pterynotus* s.s. includes four different species lineages, first noted by Harasewych and Jensen (1979) and later expanded (Vokes, 1992, p. 4) to include a fifth morphotype known only from the fossil record. The species within each lineage resemble each other, but differ from the other lineages, in the nature of the apertural denticulations, the thickness and scabrousness of the shell, etc. But all seem to be sufficiently closely related to be included within a single taxon. For this reason I separated the western Atlantic species into "species groups" (Vokes, 1992).

The geologically earliest group (Group 1) is that of *Pterynotus guesti* Harasewych and Jensen, 1979, in which there is a narrow channel in the varical shoulder spine. But in these species the aperture does not open into the spine and there are denticles on the inner side of the outer lip. This group goes back to the American Paleocene *P. matthewsensis* (Aldrich, 1886) and includes two Recent species: *P. guesti*, from off Florida, and *P. vespertilio* (Kira, 1959), from Japan. It is this group that has the greatest similarity to the subgenus *Pterochelus*, being distinguished primarily by the way the apertural lip does not open into the posterior spine, and by the denticulate aperture.

Group 2, that of *P. tricarinatus* (Lamarck, 1803), is known only from the fossil record, and is characterized by having a denticulate aperture, which folds into a small shoulder spine. The shells are also slightly scabrous and the members are clearly intermediate between the group of *P. guesti* (Group 1) and the typical group (Group 3) of *P. pinnatus*, which has an extremely scabrous shell, no shoulder spine, and only weak apertural denticles. The group (Group 4) of *P. phaneus* (Dall, 1889) consists of those extremely delicate smooth shells, with only weak apertural denticles, for which the generic name *Timbellus* de Gregorio, 1885 (type species: *Murex latifolius* Bellardi, 1872) has been proposed.

The last group (Group 5) is that of *P. phyllopterus* (Lamarck, 1822), with heavy, smooth shells and no shoulder spines, but very heavy apertural denticulations. This group extends back to the Oligocene of Mississippi, and includes the Recent Australian *P. bednalli* (Brazier, 1878).

In summary, Table 1 shows the distribution of the various characters among the five species groups of *Pterynotus*. Comparison with the subgenus *Pterochelus* shows that there is no single distinguishing character. Nevertheless, the phylogenetic history of a channeled, strong shoulder spine, seems to me to be worthy of recognition at the subgeneric level.

Pterynotus (Pterochelus) acanthopterus (Lamarck)

Plate 1, figures 1-4; Plate 2, figures 1-4; Plate 3, figures 1, 2

Murex acanthopterus Lamarck, 1816, Encycl. Méth., v. 3, pl. 417, fig. 2; Le Liste, p. 5; Kiener, 1842, Coq. Vivante, Rocher, p. 105, pl. 38, fig. 2; Sowerby, 1841, Conch. Illus., *Murex*, fig. 85; Reeve, 1845, Conch. Icon., v. 3, *Murex*, pl. 16, fig. 64; Sowerby, 1879, Thes. Conch., v. 4, *Murex*, pl. 10, fig. 90; pl. 13, fig. 127.

Table 1. Comparison of shell characters in the "species groups" of *Pterynotus* s.s., with those of *Pterochelus*.

	Group 1 <i>P. guesti</i>	Group 2 <i>P. tricarinatus</i>	Group 3 <i>P. phaneus</i>	Group 4 <i>P. phyllopterus</i>	Group 5 <i>P. pinnatus</i>	<i>Pterochelus</i>
shoulder spine	X	X				X
weak or no apertural denticulations			X		X	X
strong apertural denticulations	X	X		X		
smooth surface	X		X	X		X
scabrous surface		X			X	X
thin shell	X		X			X
heavy shell		X		X	X	X

Murex (*Pteronotus*) *acanthopterus* Lamarck. Watson, 1885, *Challenger*, Rept. Sci. Results, Zoology, v. 15, pt. 2, p. 155.

Murex (*Pteronotus*) *saibaiensis* Melvill and Standen, 1899, *J. Linn. Soc. Zool.*, v. 27, p. 161, pl. 10, fig. 1.

Pterynotus (*Pterochelus*) *acanthopterus* (Lamarck). Ponder, 1972, *J. Malac. Soc. Aust.*, v. 2, no. 3, p. 216, pl. 20, fig. 2 (Broome form), text-fig. 1:2a, 2b (radula, Broome form); Ponder and Wilson, 1973, *J. Malac. Soc. Aust.*, v. 2, no. 4, p. 396, pl. 39, fig. 1; Wilson and Gillett, 1974, *Australian Shells*, p. 88, pl. 59, figs. 4, 4b only (fig. 4a = *P. akation*, n. sp.); Wilson and Gillett, 1979, *Field Guide Australian Shells*, p. 147, pl. 33, figs. 4, 4b only (fig. 4a = *P. akation*, n. sp.).

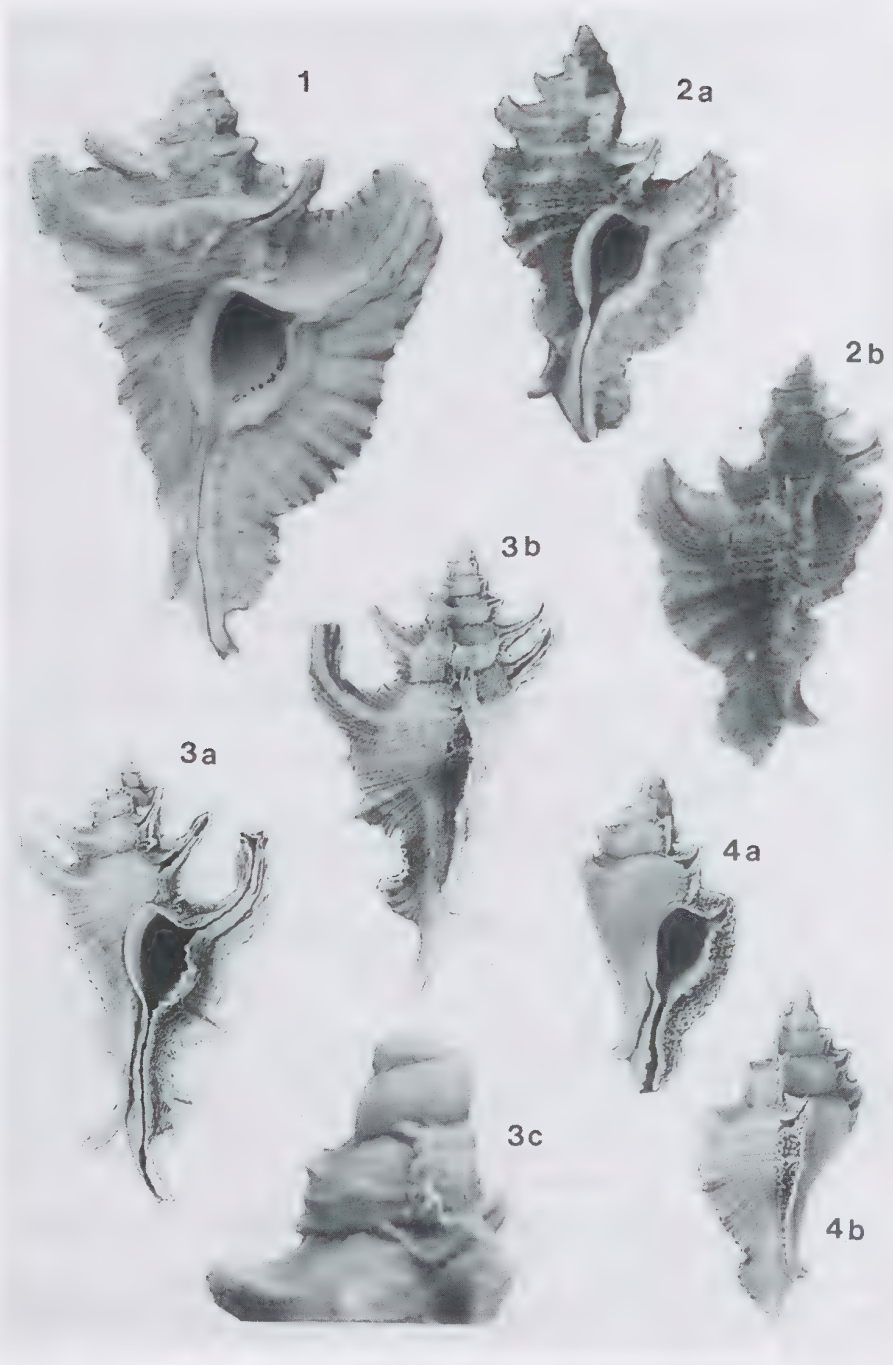
Pterochelus *acanthopterus* (Lamarck). Radwin and D'Attilio, 1976, *Murex Shells of the World*, p. 95, pl. 15, figs. 1, 2 only (fig. 3 = *P. akation*, n. sp.); Fair, 1976, *The Murex Book*, p. 17, pl. 14, fig. 181; Wells and Bryce, 1986, *Seashells Western Australia*, p. 88, pl. 25, fig. 286; Vokes, 1989, *Amer. Conchologist*, v. 17, no. 2, p. 5, text-fig. 3 only (text-fig. 7 = *P. undosus*, n. sp.).

Pterochelus *saibaiensis* (Melvill and Standen). Kaicher, 1980, *Card Catalogue World Wide Shells*, Pack 25, Muricidae, Part V, no. 2559 (holotype).

Type material: Holotype: Lamarck Collection, Muséum d'Histoire Naturelle Geneve; length 67 mm (*vide* Kiener, 1843, p. 105).

Type locality: Not known.

Material examined: The collections of the Australian Museum, the Western Australian Museum, the British Museum (Natural History), and many private collections throughout Australia and the United States.



Geographic range: From Cape York Peninsula, Queensland, to north of Rottneet Island, Western Australia.

Discussion: The original illustration of *Murex acanthopterus* by Lamarck is instantly recognizable. Moreover, the illustration given by Kiener (1842, pl. 38, fig. 2) is either of the same specimen or a copy of Lamarck's illustration (the back view of the shell is turned slightly in Kiener's illustration, suggesting that it is actually another rendering of the same specimen rather than just a copy). According to Watson (1885, p. 155) and Hedley (1913, p. 327), the holotype of *P. acanthopterus* is in the Geneva Muséum d'Histoire Naturelle. Watson also noted that the type specimen has been badly acid-etched and has lost the varical flanges through breakage.

The illustration given by Sowerby in the *Conchological Illustrations* (1841) was subsequently copied in both Reeve (1845) and Sowerby in the *Thesaurus Conchyliorum* (1879, pl. 10, fig. 90). There have been numerous illustrations of this long known species and those cited here are only intended to be a representative sample.

In spite of the fact that the species was recognized by all early workers, for years no one had any idea of provenance. The first to cite a locality was Angas (1867, p. 186), who listed *Murex acanthopterus* from Watson's Bay, a error for the species subsequently named *Pterochelus duffusi* by Iredale. Sowerby (1879, expl. pl. 10) listed the locality as "Australia," almost certainly following Angas and, thus, technically incorrect. Watson (1885, p. 155) first correctly reported the species from northern Australia.

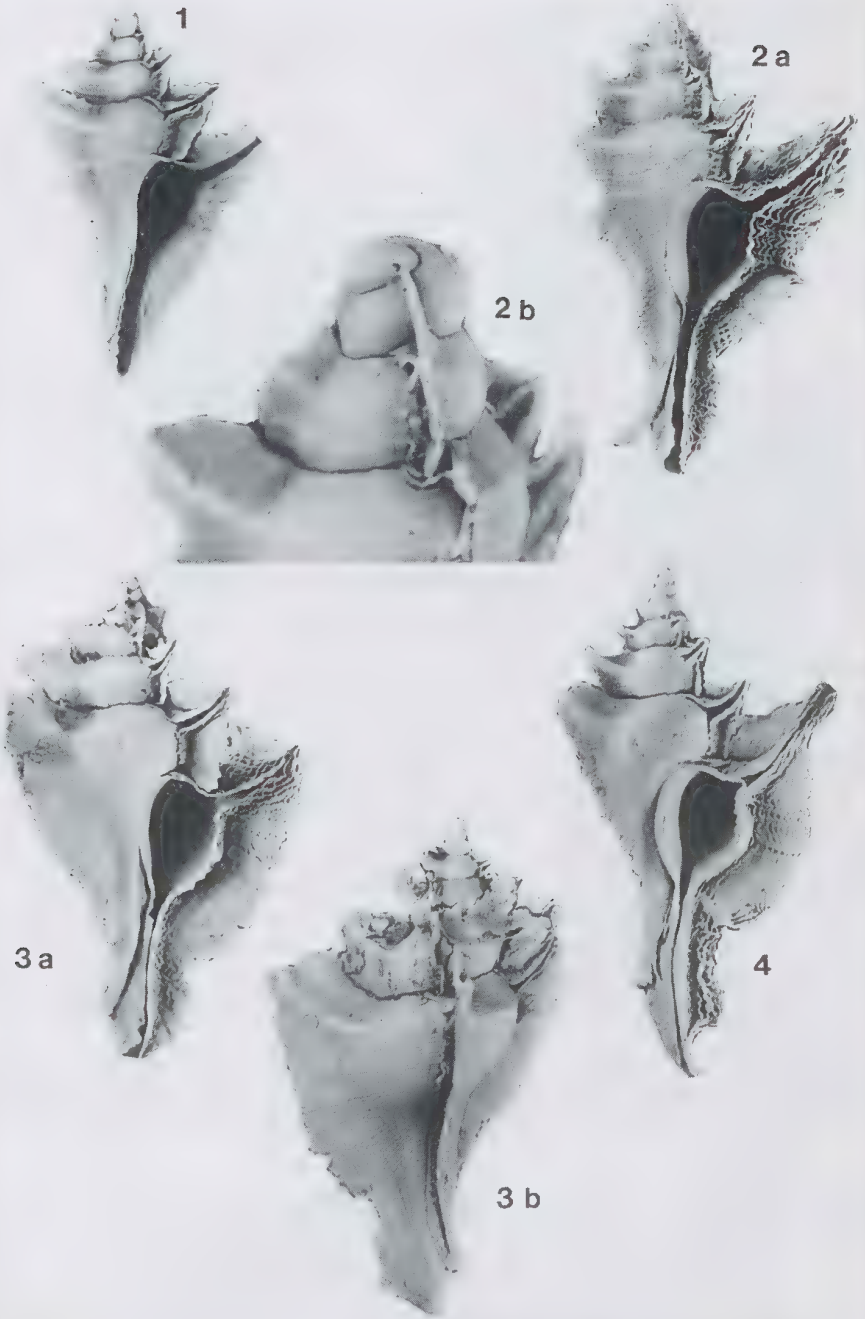
The eastern limit of the range of *P. acanthopterus* is usually cited as the Kimberley Range (Wilson and Gillett, 1974, p. 88; 1979, p. 147; Wells and Bryce, 1986, p. 88). But, in the collections at the Australian Museum, there are examples from as far east as Darwin and Arnhem Land (AMS C 77055, Boucart Bay, Arnhem Land).

Watson, in the *Challenger* Report (1885, p. 155) recorded *P. acanthopterus* from Station 187, just west of the Cape York Peninsula, in 6 fathoms [11 meters]. Subsequently Melville and Standen (1899, p. 161, pl. 10, fig. 1) named a small specimen from the Torres Strait *Murex (Pteronotus) saibaiensis*, for the type locality at Saibai Island, just off the south coast of Papua New Guinea, where the holotype (BMNH 1899.2.23.25; refigured here, pl. 2, fig. 1) was taken in 10-17 fathoms [18-31 meters].

In 1913 Hedley (p. 327) dismissed *M. saibaiensis* as a synonym of *P. acanthopterus* and no one has mentioned it since, until Kaicher (1980, no. 2559) refigured the holotype. The shell is obviously a juvenile with only four post-nuclear whorls and is triangular in outline, lacking the characteristic "notch" along the anterior portion of the varical flange. But this is simply a function of size, for this notch is not well-developed in juvenile shells, only becoming present on about the fifth teleoconch whorl (see pl. 1, fig. 4). Comparison with the adult specimen reported by Watson (1885, p. 155; BMNH 1887.2.9.538; figured here, pl. 2, fig. 2) indicates that both are to be referred to *P. acanthopterus*.

More recently, a number of specimens have been dredged in the Gulf of Carpenteria and the Torres Strait. In material dredged off Badu Island an adult specimen (pl. 2, fig. 3) is of the more triangular "*saibaiensis*" type but has the characteristic notch in the

- ◀ **Plate 1.** Figures 1-4. *Pterynotus (Pterochelus) acanthopterus* (Lamarck, 1816). 1. Vokes Coll.; length 85.2 mm, width 46.2 mm; locality, Dampier, W.A., low tide (X 1; shell not whitened, to show color pattern). 2. WAM 238-93; length 43.6 mm, width 24.6 mm; locality, Dampier, W.A., low tide (X 1 1/4; shell not whitened, to show color pattern). 3. AMS C 149226; length 47.5 mm, width 23.5 mm; locality, 74 mi [120 km] north-north-east of Port Hedland, W.A., 80 m (X 1 1/4; protoconch X 10). 4. AMS C 172776; length 21.4 mm; width 9.5 mm; locality, Port Hedland, W.A., on reef at low tide (X 2).



varix. In the same dredge haul, there are other examples of the typical "*acanthopterus*" morphology (pl. 2, fig. 4). Thus, the eastern limit of the range of *P. acanthopterus* should be extended as far as the Torres Strait.

In the vicinity of Broome, Western Australia (figured by Ponder, 1972a, pl. 20, fig. 2; refigured here pl. 3, fig. 2), there is another form that differs somewhat from the typical *P. acanthopterus* and may prove to be a different species. It is always smaller (maximum length 40 mm) and sometimes has a brown and white banded color pattern. It is this form that is truly the "dwarf" *P. acanthopterus* and, for the present, it is considered to be no more than that.

***Pterynotus* (*Pterochelus*) *triformis* (Reeve)**

Plate 3, figures 3-6

Murex acanthopterus var. Sowerby, 1841, Conch. Illus., *Murex*, fig. 51.

Murex triformis Reeve, 1845, Conch. Icon., v. 3, *Murex*, pl. 13, fig. 53; Reeve, 1846, Proc. Zool. Soc. London, pt. 13, p. 87; Sowerby, 1879, Thes. Conch., v. 4, *Murex*, pl. 10, fig. 92, pl. 13, fig. 126.

Pterynotus (*Pterochelus*) *triformis* (Reeve). Ponder, 1972, J. Malac. Soc. Aust., v. 2, no. 3, p. 216, text-figs. 4:32, 4:33 (operculum, fig. 4:32 is reversed); Ludbrook, 1978, Geol. Surv. W.A., Bull. 125, p. 142, pl. 15, figs. 17, 18; Wilson and Gillett, 1974, Australian Shells, p. 88, pl. 59, figs. 1, 1a, 1b; Wilson and Gillett, 1979, Field Guide Australian Shells, p. 147, pl. 33, figs. 1, 1a, 1b.

Pterochelus triformis (Reeve). Radwin and D'Attilio, 1976, *Murex Shells of the World*, p. 97, pl. 15, fig. 7 only (fig. 6 = *P. undosus*, n. sp.); Fair, 1976, *The Murex Book*, p. 82, pl. 14, fig. 182; Wells and Bryce, 1986, *Seashells Western Australia*, p. 88, pl. 26, fig. 291; Vokes, 1989, *Amer. Conchologist*, v. 17, no. 2, p. 3, text-figs. 2, 6.

Type material: Holotype: National Museum of Victoria, no. F 30968; length 58.6 mm, width 32.3 mm.

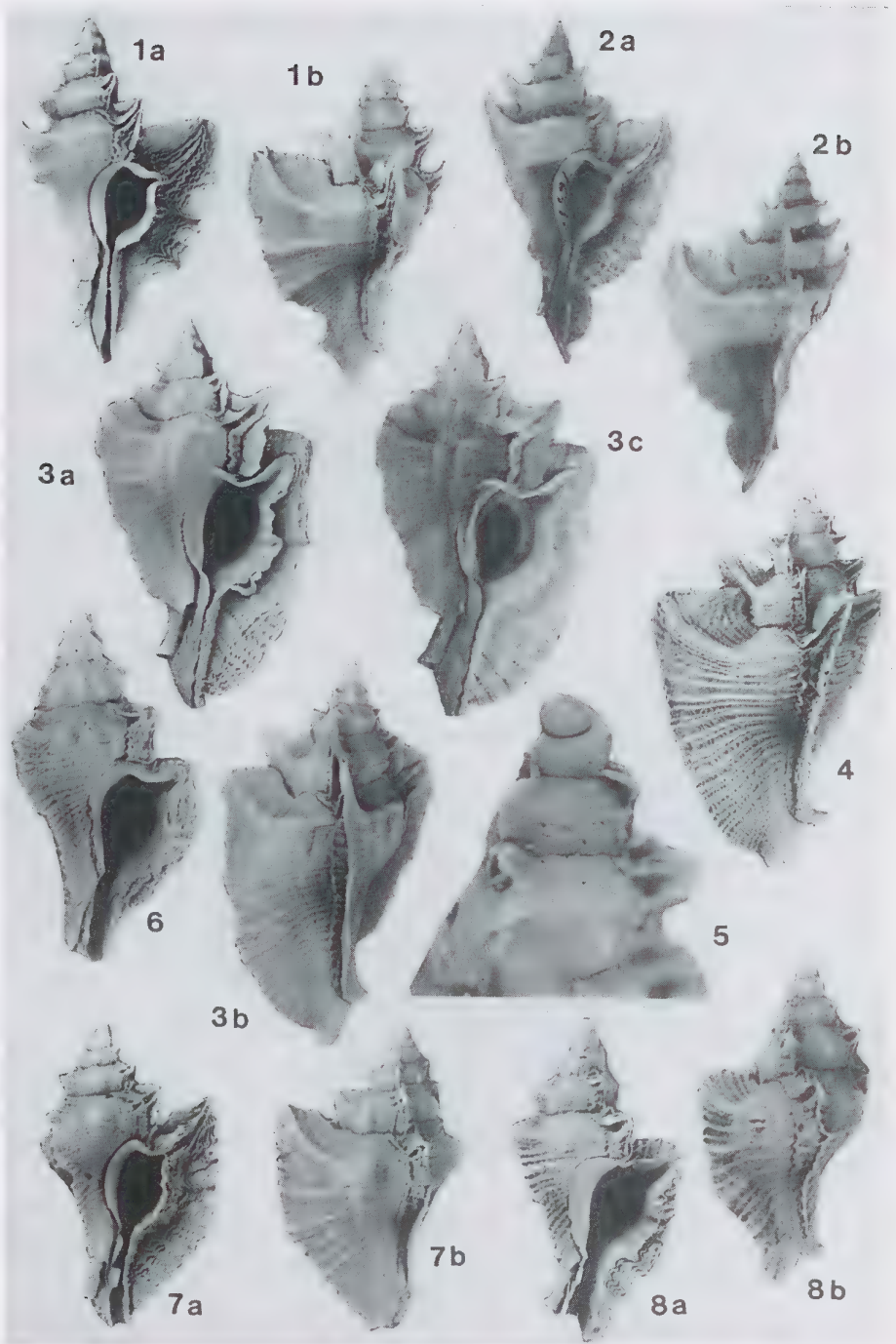
Type locality: "New Holland."

Material examined: The collections of the Australian Museum, the Western Australian Museum, the National Museum of Victoria, the South Australian Museum, the British Museum (Natural History), and many private collections throughout Australia and the United States.

Geographic range: From southernmost New South Wales, Bass Strait, and Tasmania to Esperance, Western Australia.

Discussion: Along the southern coast of Australia, the species of *Pterochelus* that occurs from New South Wales and Tasmania to the eastern part of Western Australia is *P. (P.) triformis* (Reeve). The western extent of the range of this species has been said to be Albany, W.A. (Wilson and Gillett, 1974, p. 88; 1979, p. 147; Radwin and D'Attilio, 1976, p. 96) or even Cape Naturaliste, W.A. (Wells and Bryce, 1986, p. 88). But all of the specimens I have seen coming from west of Esperance, W.A., such as that figured as *P. triformis* by Radwin and D'Attilio (1976, pl. 15, fig. 6), are *P. undosus*, n. sp., as is discussed below.

- ◀ **Plate 2. Figures 1-4.** *Pterynotus* (*Pterochelus*) *acanthopterus* (Lamarck, 1816). 1. BMNH 1899.2.23.25 (holotype — *Murex saibaiensis* Melvill and Standen); length 17.8 mm, width 9.6 mm; locality, Saibai Island, Papua New Guinea, 10-17 fm [18-31 m] (X 3). 2. BMNH 1887.2.9.538; length 31.1 mm, width 18.5 mm; locality, *Challenger* Station 187, just west of Cape York Peninsula, 6 fm [11 m] (X 2; protoconch X 10). 3. Lamprell Coll.; length 48.2 mm, width 25.9 mm; 10°12'S, 141°51.53'E, Torres Strait, 46 m (X 1 1/4). 4. Lamprell Coll.; length 50.2 mm, width 23.8 mm; locality same as fig. 3 (X 1 1/4).



Although both are taken at Esperance, the two species do not actually occur together. *Pterynotus triformis* is found in the more sheltered area of the rocks of the man-made groyne but *P. undosus* occurs offshore in more open (rougher) and slightly deeper water (ca. 30 m).

Pterynotus (*Pterochelus*) *duffusi* (Iredale)

Plate 4, figures 1-5

Murex acanthopterus Lamarck. Angas, 1867, Proc. Zool. Soc. London, (1867), p. 186 (not of Lamarck).

Pterochelus duffusi Iredale, 1936, Rec. Australian Mus., v. 19, p. 323, pl. 23, fig. 11; Radwin and D'Attilio, 1976, Murex Shells of the World, p. 96, pl. 15, fig. 5, text-figs. 60 (protoconch), 61 (radula); Vokes, 1989, Amer. Conchologist, v. 17, no. 2, p. 3, text-figs. 1, 13 (holotype).

Pterynotus (*Pterochelus*) *phillipsi* Vokes, 1966, Veliger, v. 8, no. 3, p. 165, pl. 25, figs. 1, 2.

Pterynotus (*Pterochelus*) *duffusi* (Iredale). Vokes, 1966, Veliger, v. 8, no. 3, p. 166, pl. 25, fig. 3; Wilson and Gillett, 1974, Australian Shells, p. 88, pl. 59, fig. 8; Wilson and Gillett, 1979, Field Guide Australian Shells, p. 148, pl. 33, fig. 8.

Pterochelus phillipsi (Vokes). Radwin and D'Attilio, 1976, Murex Shells of the World, p. 97, text-fig. 62 (holotype); Fair, 1976, The Murex Book, p. 67, pl. 14, fig. 183 (holotype); Vokes, 1989, Amer. Conchologist, v. 17, no. 2, p. 5, text-fig. 12 (holotype).

Not *Pterochelus duffusi* Iredale. Fair, 1976, The Murex Book, p. 38, pl. 14, figs. 184, 184a (= *P. undosus*, n. sp.).

Pterochelus sp. cf. *acanthopterus* (Lamarck). Vokes, 1989, Amer. Conchologist, v. 17, no. 2, p. 3, text-fig. 5.

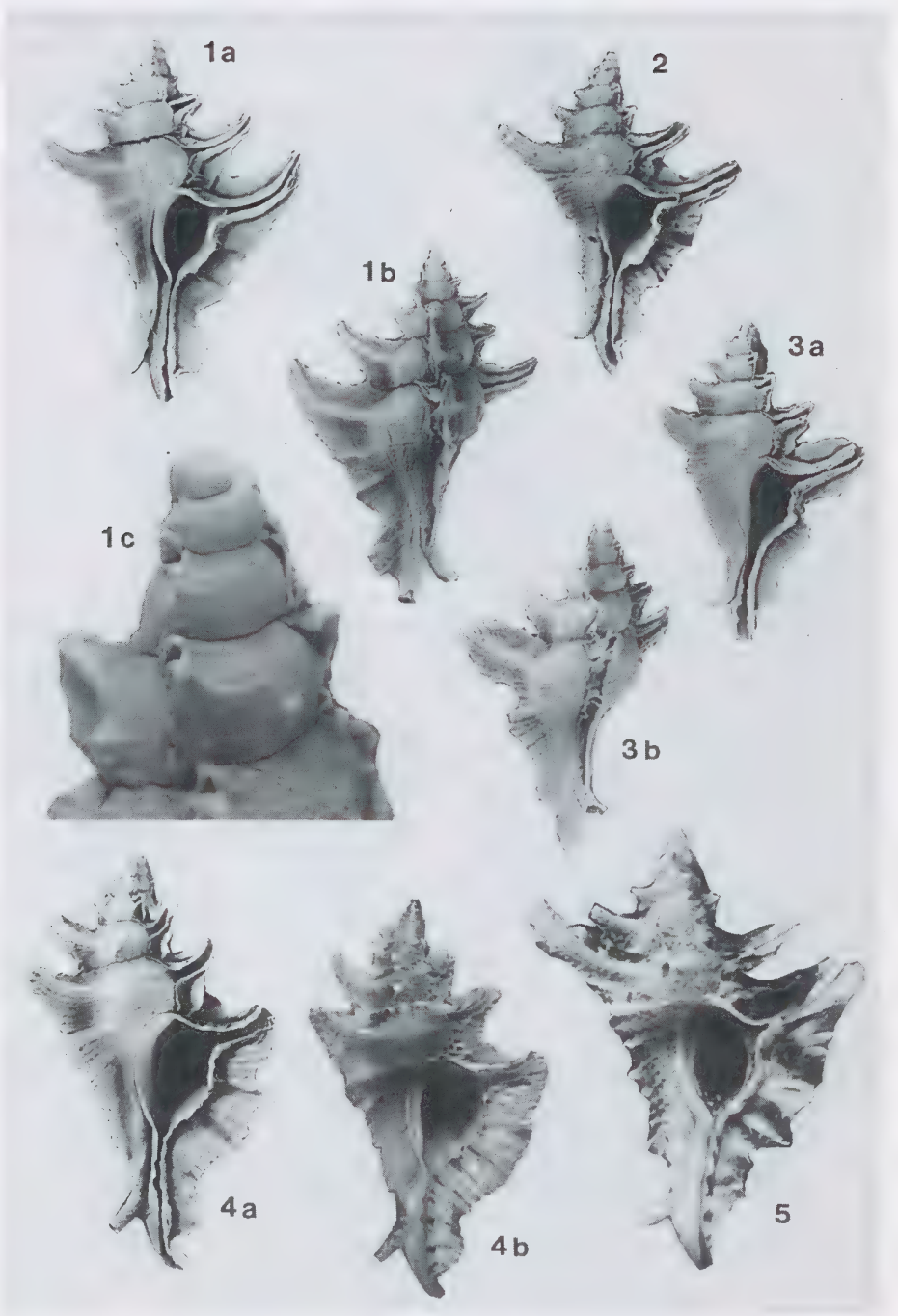
Type material: Holotype: AMS C 60674; length 27.0 mm, width 18.6 mm. SBNHM 22190 (holotype — *P. phillipsi* Vokes); length 28.4 mm, width 18.0 mm; locality, "off Santa Barbara, California, 100 fm [182 m]."

Type locality: Broken Bay, New South Wales.

Material examined: The collections of the Australian Museum, the Western Australian Museum, the National Museum of Victoria, the South Australian Museum, the British Museum (Natural History), and many private collections throughout Australia and the United States.

Geographic range: Moreton Bay, Queensland, to (?) Port Macdonnell, South Australia.

- ◀ **Plate 3.** Figures 1-2. *Pterynotus* (*Pterochelus*) *acanthopterus* (Lamarck, 1816). 1. AMS C 76582; length 36.8 mm, width 19.8 mm; locality, Broome, W.A., low tide (X 1 1/4). 2. AMS C 76582A; length 37.7 mm, width 18.5 mm; locality, Broome, W.A., low tide (X 1 1/4); shell not whitened, to show color pattern). 3-6. *Pterynotus* (*Pterochelus*) *triformis* (Reeve, 1845). 3. WAM 229-93; length 55.4 mm, width 28.3 mm; locality, South Australia (X 1; fig. 3c not whitened, to show color pattern). 4. WAM 234-93; length 46.0 mm, width 25.3 mm; locality, Taylor Street groyne, Esperance, W.A. (X 1 1/4). 5. WAM 235-93; length 14.0 mm, width 7.8 mm; locality, Taylor Street groyne, Esperance, W.A. (X 10). 6. Vokes Coll.; length 37.8 mm, width 19.7 mm; locality, Roe Calcaranite, Eucla, W.A. (X 1 1/4). 7. *Pterynotus* (*Pterochelus*) *westralis* Ponder and Wilson, 1973. WAM 373-72; length 28.8 mm, width 18.0 mm; locality, off Dongara, W.A., 130-146 m (X 1 1/2). 8. *Pterynotus* (*Pterochelus*) *ariomus* (Clench and Pérez Farfante, 1945). MCZ 164734 (holotype); length 22.6 mm; width 12.4 mm; locality, off Hollywood, Florida, in 50-60 fm [91-110 m] (X 2).



Discussion: The holotype of *P. (P.) phillipsi* was said to have been taken live in a fish trawl off Santa Barbara, California, in approximately 100 fathoms [182 meters] depth. Although I named it as a new species, comparing it to the Australian *P. duffusi*, I noted that there were only slight differences. In the ensuing years no additional specimens of *P. phillipsi* have been collected off California. After examination of additional material of *P. duffusi*, I now feel confident that the American specimen was mislocalized, for it is identical to examples of *P. duffusi* (compare pl. 4, figs. 2, 3) from Australia.

As a corroboration of this mislocalization, when the question about the locality of the holotype was raised, Dr. Henry W. Chaney, Santa Barbara Museum of Natural History, offered to examine the colony of Bryozoa encrusting the shell. He advises (personal communication, April, 1993) that the bryozoan colony is definitely a Queensland species, although the exact taxon is still in systematic question.

At the time of the description, I also figured a specimen of what I considered to be *P. duffusi* (Vokes, 1966, pl. 25, fig. 3) from off Eden, N.S.W. This specimen (refigured herein, pl. 4, fig. 4) is not typical of *P. duffusi*, which usually is characterized by extremely elongated shoulder spines. In some ways this Eden specimen resembles the more westerly *P. undosus*, n. sp.; however, it has a smoother shell surface than specimens of *P. undosus* and also has a larger protoconch, like that of *P. duffusi*. In spite of the superficial similarity to *P. undosus*, I believe it is no more than an atypical specimen of *P. duffusi*.

In general, specimens of *P. duffusi* from the northern end of the range are smaller (maximum length 40 mm) and smooth, in contrast to those from the southeastern portion of the continent, where they are larger (50-55 mm in length) and have a malleated texture to the shell surface.

In the collections of Mr. Ian Campbell, of Port Macdonnell, S.A., there are several specimens (some living in his marine aquarium as recently as December, 1991) of an unusual form (pl. 4, fig. 5) with an intense color pattern and a very scabrous surface. They are similar to *P. undosus* in the scabrous surface and the intense color pattern; however, the elongated shoulder spines are more like those of *P. duffusi*. In view of the disjunct distribution I tentatively consider the Port Macdonnell specimens to be referable to *P. duffusi*.

Pterynotus (*Pterochelus*) *westralis* Ponder and Wilson

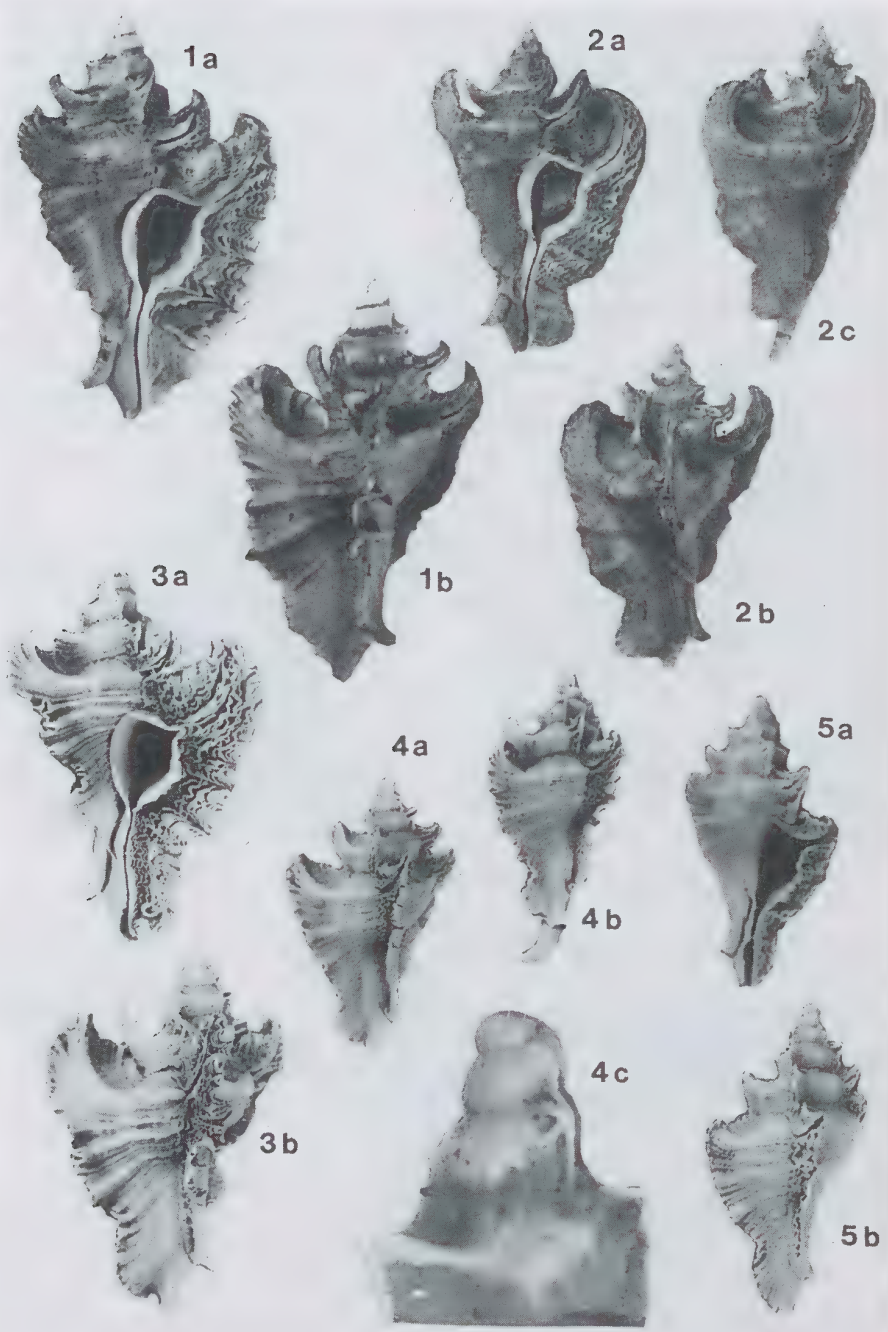
Plate 3, figure 7

Pterynotus (*Pterochelus*) *westralis* Ponder and Wilson, 1973, J. Malac. Soc. Aust., v. 2, no. 4, p. 396, pl. 39, figs. 2, 3 (not 1, as cited); text-figs. 1, 2 (radula).

Pterynotus westralis Ponder and Wilson. Wells and Bryce, 1986, Seashells Western Australia, p. 88, pl. 26, fig. 290.

Pterochelus westralis (Ponder and Wilson). Vokes, 1989, Amer. Conchologist, v. 17, no. 2, p. 5, text-fig. 8 (paratype).

- ◀ **Plate 4.** Figures 1-5. *Pterynotus* (*Pterochelus*) *duffusi* (Iredale, 1936). 1. WAM 233-93; length 33.3 mm, width 20.0 mm; locality, off Cape Moreton, Qld., 100 fm [182 m] (X 1 1/2; protoconch X 10). 2. SBNHM 22190 (holotype — *P. phillipsi* Vokes); length 28.4 mm, width 18.0 mm; locality, "off Santa Barbara, California, 100 fm [182 m]" ((X 1 1/2). 3. AMS C 173362; length 28.5 mm, width 17.0 mm; locality, off Eden, N.S.W. (X 1 1/2). 4. Vokes Coll., length 46.0 mm, width 27.5 mm; locality, off Eden, N.S.W., 60 fm [110 m] (X 1 1/4; fig. 4b not whitened, to show color pattern). 5. Campbell Coll.; length 50.1 mm, width 29.3 mm; locality, Port Macdonnell, S.A. (X 1 1/4; shell not whitened, to show color pattern).



Type material: Holotype: WAM 438-72; length 28.0 mm, width 15.4 mm (*vide* Ponder and Wilson, 1973, p. 400).

Type locality: Northwest of Rottnest Island, W.A., dredged in 146 m, fine calcareous sand substrate.

Material examined: The type lot in the collections of the Australian Museum and the Western Australian Museum.

Geographic range: Western Australia, from North West Cape to Bunbury.

Discussion: *Pterynotus* (*Pterochelus*) *westralis* Ponder and Wilson is confined to the western coast of Australia from Bunbury, near the southwestern corner, to North West Cape (Wells and Bryce, 1986, p. 88). It is a deep-water form, occurring in depths ranging from 115 to 221 meters (Ponder and Wilson, 1973, p. 398) and, as noted by the original authors, is sometimes taken in the same dredge hauls as *P. acanthopterus* north of Rottnest Island. It is a relatively small species, with maximum length of only 31 mm, and lacks the "typical" notch along the anterior portion of the varical flange.

Pterynotus (*Pterochelus*) *akation* Vokes, n. sp.

Plate 5, figures 1-5

Pterynotus (*Pterochelus*) *acanthopterus* (Lamarck). Wilson and Gillett, 1974, Australian Shells, p. 88 (in part), pl. 59, fig. 4a (only); Wilson and Gillett, 1979, Field Guide to Australian Shells, p. 147 (in part), pl. 33, fig. 4a (only).

Pterochelus acanthopterus (Lamarck). Radwin and D'Attilio, 1976, Murex Shells of the World, p. 96, pl. 15, fig. 3 (only).

Pterochelus acanthopterus "dwarf form." Vokes, 1989, Amer. Conchologist, v. 17, no. 2, p. 5, text-fig. 4.

Description: Shell with protoconch of one and one-half smooth whorls, teleoconch of six to seven whorls. Spiral ornamentation lacking on earliest teleoconch; on about third post-nuclear whorl a strong angulation at shoulder and by fourth whorl faint spiral threads developed, covering entire exterior surface of shell. On body whorl three raised cords, one at shoulder, a second at base of body whorl, and a third half-way between these two. Axial ornamentation from earliest post-nuclear whorls of three flanged varices, each with open channel within adapically recurved shoulder spine. Varical flange extending along entire length of shell to near tip of siphonal canal. Apertural faces of varices constructed of multiple layers of thin shelly material, each intricately recurved to reflect strength of spiral ornamentation, with larger abapertural folds at two major cords, and a more diffuse recurved area forming a "notch" at base of body whorl. One strong intervarical node between each pair of varices, beginning about second teleoconch whorl; on adult body whorl single nodes breaking down to two or three smaller nodes. Entire shell covered by numerous growth lamellae giving a scabrous surface. Suture slightly impressed, subsutural area imbricated by growth lamellae. Aperture pyriform, wider at posterior end; inner lip smooth, lightly appressed at posterior but free-standing along most of length. Inner side of outer lip smooth, outer

- ◀ **Plate 5.** Figures 1-5. *Pterynotus* (*Pterochelus*) *akation* Vokes, n. sp. 1. WAM 230-93 (holotype); length 44.4 mm, width 25.2 mm (X 1 1/4; shell not whitened, to show color pattern). 2. WAM 232-93 (paratype A); length 37.9 mm, width 21.4 mm (X 1 1/4; shell not whitened, to show color pattern). 3. AMS C 172400 (paratype B); length 37.4 mm, width 22.5 mm (X 1 1/4). 4. AMS C 172401 (paratype C); length 26.0 mm, width 14.1 mm (X 1 1/2; protoconch X 10). Locality of all, Dampier, W.A., on reef at low tide. 5. AMS C 173363 (paratype D); length 19.8 mm, width 10.3 mm; locality, Port Hedland, W.A., on reef at low tide (X 2).

edge crenulated to reflect spiral ornamentation; small sharp teeth between emarginations formed by major cords. Outer margin folded into channel at shoulder spine. Siphonal canal moderately long, straight, almost closed but open by a narrow slit; recurved at distal end. Color yellowish-brown, generally lighter on apertural faces; rare examples with broad white band between shoulder and base of body whorl. Operculum unguiculate, with terminal nucleus (as shown in Ponder, 1972a, text-fig. 4:32).

Type material: Holotype: WAM 230-93; length 44.4 mm, width 25.2 mm (coll. Joe Rinkens). Paratypes: WAM 232-93 (paratype A); length 37.9 mm, width 21.4 mm. AMS C 172400 (paratype B); length 37.4 mm, width 22.5 mm. AMS C 172401 (paratype C); length 26.0 mm, width 14.1 mm. Locality of all, Dampier, W.A., on reef at low tide (coll. Joe Rinkens). AMS C 173363 (paratype D); length 19.8 mm, width 10.3 mm, locality, Port Hedland, W.A., on reef at low tide (*ex* Seymour Coll.).

Another 12 specimens in the Vokes Collection.

Type locality: Dampier, Western Australia, on reef exposed at low tide.

Etymology of name: *akation* (Gr.) — a dwarf.

Geographic range: North coast of Western Australia, from Cape Keraudren to Onslow.

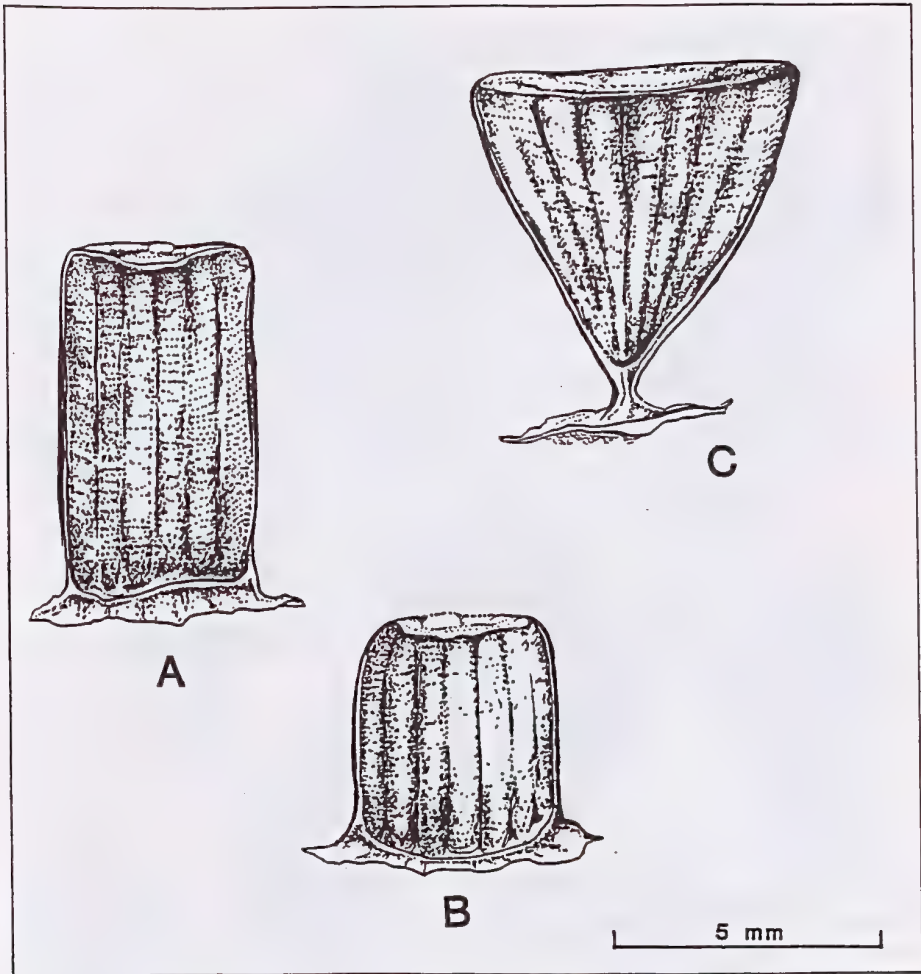
Discussion: For some time collectors have been aware of the existence of an undescribed species of *Pterochelus* in northwestern Australia, usually cited as "dwarf form of *P. acanthopterus*" (*e.g.*, Wilson and Gillett, 1974, p. 88; 1979, p. 147; Radwin and D'Attilio, 1976, p. 96). In a popular article on the species of *Pterochelus* (Vokes, 1989, p. 5) I noted that this species was in need of a name; however, with little more information than the fact of its occurrence in the area from Port Hedland to Dampier, I was reluctant to consider it as a new species. There was always the possibility that it is no more than an ecologic variant of the more widespread *P. acanthopterus*, perhaps induced by hypersalinity of the nearby salt-pans in the Dampier region. Perhaps it is an example of sexual dimorphism, as suggested by Wilson and Gillett (1974, p. 88; 1979, p. 147).

However, a trip to the Port Hedland-Dampier region in May, 1992, provided me with sufficient answers to my questions to show that this "dwarf form" is a valid species, sympatric but not intergrading with typical *P. acanthopterus*.

In Port Hedland Mr. Joe Rinkens, local collector and shell-dealer provided me with information on the habits of the two species in question. According to him, the two forms live together on the reefs exposed at low tide, although *P. acanthopterus* is found in deeper water as well (Ponder and Wilson, 1973, p. 400, list depths averaging 179 meters for dredged specimens of *P. acanthopterus* in the Western Australian Museum). There are presumably some micro-ecological differences between the two forms, but they are not immediately obvious.

The spawning habits are similar, both produce clusters of individual egg-capsules cemented to the inner side of bivalve shells. However, those of *P. (P.) acanthopterus* are roughly cylindrical, approximately twice as high as they are wide (text-figure 1A) but those of the new species are more rounded on top and approximately equidimensional in height and diameter (text-figure 1B). Neither species has the "typical" muricine vase-shaped capsule seen in *P. (P.) triformis* (text-figures 1C, 2).

The range of *P. (P.) akation*, although overlapping typical *P. acanthopterus*, is much more restricted, occurring only in northern Western Australia, from Onslow (AMS C 95844; Thevenard Island), *ca.* 400 km west of Port Hedland, to Cape Keraudren, 140 km east of Port Hedland, or a distance of about 540 km in all. In contrast, *P. acanthopterus* has been recorded on the west coast from as far south as Rottneest Island



Text-figure 1. Egg-capsules of: (A) *Pterynotus* (*Pterochelus*) *acanthopterus*; (B) *Pterynotus* (*Pterochelus*) *akation*, n. sp.; (C) *Pterynotus* (*Pterochelus*) *triformis*.

(Ponder and Wilson, 1973, p. 400, pl. 39, fig. 1) and on the north coast as far east as the Torres Strait.

This species surprisingly has remained undescribed in spite of being recognized as "different" from the sympatric *P. acanthopterus* since at least 1974 (Wilson and Gillett, p. 88). From the latter it differs not only in the obvious smaller size (maximum length about 45 mm) and the stronger angulation at the shoulder but also in the more adapically recurved shoulder spines, which are relatively shorter, and a lower spire relative to *P. acanthopterus*. The color in the new species is also distinctive for, although *P. acanthopterus* varies from almost white to dark brown, it never has the yellowish-brown color seen in *P. akation*.

Juvenile specimens of *P. (P.) acanthopterus* may be mistaken for this new species, but close comparison permits the two to be separated on the basis of the more recurved



shoulder spines and the stronger angulation at the shoulder of *P. akation* (compare pl. 1, fig. 4 and pl. 5, fig. 5). Often the color is the easiest way to separate the two, even though this has no taxonomic validity. Most specimens of *P. akation* have a characteristic yellow-brown hue; however, there are rare examples from both Port Hedland (AMS, *ex* Coleman Coll.) and Karratha (Ignoti Coll.; Edinger Coll.) and the specimen figured by Wilson and Gillett, 1974, pl. 59, fig. 4a; 1979, pl. 33, fig. 4a) that have the brown and white banded appearance of the Broome form of *P. acanthopterus*.

From the other species of *Pterochelus* this new species is more readily distinguished. It differs from *P. duffusi* in having a more heavier and more scabrous shell, with elaborately fimbriated varical faces. From *P. triformis* it differs in lacking the widely expanded varical flange, which in the latter species is almost flat and does not show the abapertural projections of *P. akation*. In *P. triformis* the shoulder spine is not extended beyond the overall edge of the varix.

The new species *P. undosus*, which follows, is in many ways the most similar in morphology, but may be separated by the less massive shell of the latter, which also lacks the pronounced shoulder angulation. The undulating surface of the varical flange is even more well-developed in *P. undosus* (hence, the name) than in *P. akation*.

Pterynotus (*Pterochelus*) *undosus* Vokes, n. sp.

Plate 6, figures 1-5

Pterochelus triformis (Reeve). Radwin and D'Attilio, 1976, *Murex Shells of the World*, p. 97 (in part), pl. 15, fig. 6 only (fig. 7 = *P. triformis*) (*not* of Reeve).

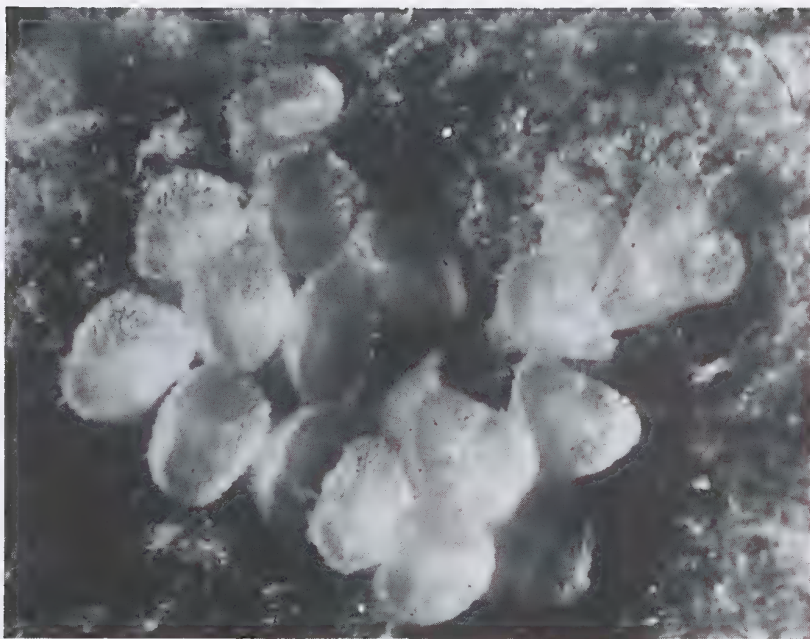
Pterochelus duffusi Iredale. Fair, 1976, *The Murex Book*, p. 38, pl. 14, figs. 184, 184a (*not* of Iredale).

Pterochelus acanthopterus (Lamarck). Vokes, 1989, *Amer. Conchologist*, v. 17, no. 2, p. 5 (in part), text-fig. 7 only (*not* of Lamarck).

Pterochelus sp. cf. *acanthopterus* (Lamarck). Vokes, 1989, *Amer. Conchologist*, v. 17, no. 2, p. 3 (map), not text-fig. 5 (= *P. duffusi*).

Description: Shell with protoconch of one and one-half smooth whorls, teleoconch of seven whorls. Spiral ornamentation from earliest teleoconch whorl onward of faint threads, gradually increasing in strength and becoming raised cords. On body whorl two cords somewhat larger, one at base of body whorl, and another half-way between that and shoulder. Axial ornamentation from earliest post-nuclear whorls of three flanged varices, each with a broad open channel within almost straight shoulder spine. Varical flange extending along entire length of shell to near tip of siphonal canal, set back from edge of apertural margin, leaving apertural margin projecting in advance of each varix. Apertural faces of varices constructed of multiple layers of thin shelly material, each intricately recurved to reflect strength of spiral ornamentation, with larger folds at two major cords, each with a long projection drawn out abaperturally, and a more diffuse recurved area forming a "notch" at base of body whorl. One narrow

- ◀ **Plate 6.** Figures 1-5. *Pterynotus* (*Pterochelus*) *undosus* Vokes, n. sp. 1. WAM 1-93 (holotype); length 54.9 mm, width 30.6 mm; locality, Dunsborough, W.A. (X 1 1/4). 2. AMS C 172398 (paratype A); length 53.8 mm, width 30.6 mm; locality, Hall's Bank, Fremantle, W.A., 10 m, under stones (X 1 1/4; shell not whitened, to show color pattern). 3. AMS C 172399 (paratype B); length 26.8 mm, width 16.1 mm; locality, same as paratype A (X 1 1/2; protoconch X 10). 4. WAM 231-93 (paratype C); length 34.8 mm, width 19.5 mm; locality, Quarantine Station, Albany, W.A., 2 m depth, on sponges (X 1 1/4). 5. Vokes Coll.; length 40.5 mm, width 17.8 mm; locality, Roe Calcarenite, Eucla, W.A. (X 1 1/4).



Text-figure 2. Egg-capsules of *Pterynotus (Pterochelus) triformis* (photograph by Neville Coleman).

“pinched-in” intervarical node between each pair of varices, beginning on second teleoconch whorl and continuing to adult body whorl. On about third teleoconch whorl numerous growth lamellae, crossing spiral cords and giving malleated appearance to entire shell surface. Suture slightly impressed, subsutural area marked by growth lamellae. Aperture oval, inner lip smooth, lightly appressed at posterior end but standing free along most of length. Inner side of outer lip smooth, outer edge crenulated to reflect spiral ornamentation; small sharp teeth between emarginations formed by major cords. Outer margin opening into broad open channel at shoulder spine. Siphonal canal moderately long, straight, almost closed but open by a narrow slit; sharply recurved at distal end. Color white, pale tan to dark brown, or occasionally peach. Frequently darker markings on subsutural ramp, darkest on abapertural side of varical flange between suture and spine, on adapertural side of intervarical nodes, and as intermittent blotches on varices, especially on that portion of apertural margin projecting in advance of the varical flange. Operculum unguiculate, with terminal nucleus (as shown in Ponder, 1972a, text-fig. 4:32). Radula typically muricine (text-fig. 3).

Type material: Holotype: WAM 1-93; length 54.9 mm, width 30.6 mm (coll. B.R. Wilson). Paratypes: AMS C 172398 (paratype A); length 53.8 mm, width 30.6 mm; locality, Hall’s Bank, Fremantle, W.A., 10 m, under stones (*ex* Coleman Coll.). AMS C 172399 (paratype B); length 26.8 mm, width 16.1 mm; locality, same as paratype A. WAM 231-93 (paratype C); length 34.8 mm, width 19.5 mm; locality, Quarantine Station, Albany, W.A., 2 m depth, on sponges (coll. Pas).

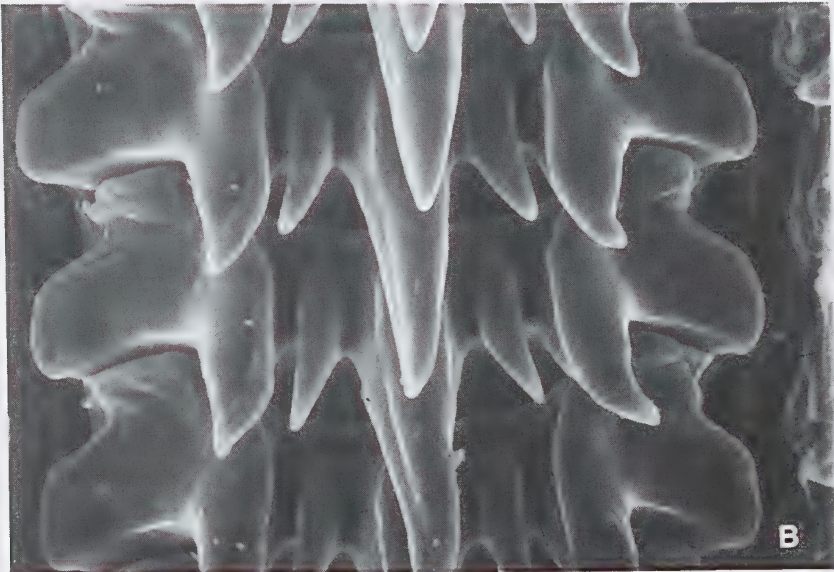
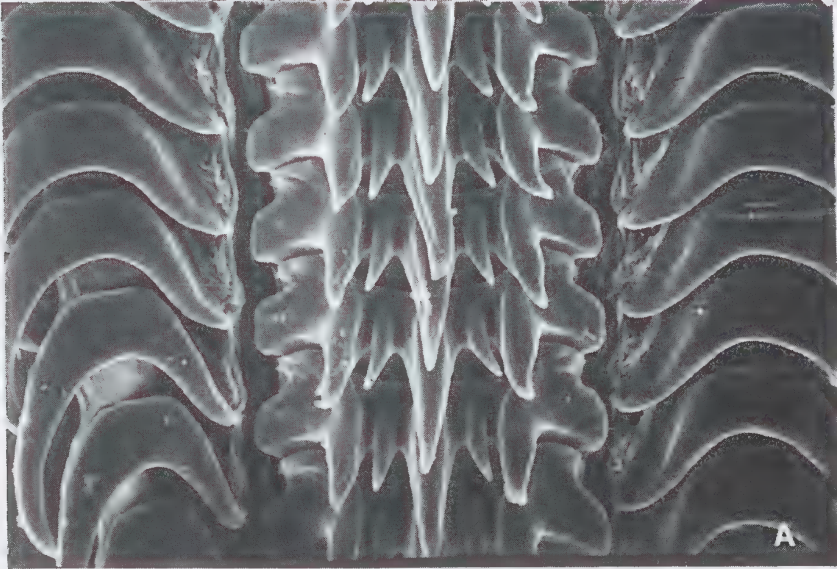
Another 23 specimens in the Vokes Collection.

Type locality: Dunsborough, Western Australia.

Etymology of name: *undosus* (Lat.) — full of waves; in reference to the edge of the varical flange.

Geographic range: Western Australia, from Perth to Esperance.

Discussion: Wilson and Gillett (1974, p. 88; 1979, p. 147) noted that along the western coast of Western Australia, between North West Cape and Cape Leeuwin, a form intermediate between *P. acanthopterus* and *P. triformis* occurs. Wells and Bryce (1986, p. 88) recorded the range of *P. triformis* as extending to the west as far as Cape Naturaliste, W.A. The specimen upon which this record is based is that one selected to be the holotype of *P. undosus*.



Text-figure 3. Radula of *Pterynotus* (*Pterochelus*) *undosus*, n. sp. (A) X 500, (B) X 1000.

Radwin and D'Attilio (1976, pl. 15, fig. 6) figured as *P. triformis* a specimen said to be from Albany, W.A. In a previous article (Vokes, 1989, p. 3), I suggested that this might be a case of mistaken locality data, for the few specimens from Albany I had seen at that time were not *P. triformis*, but an undescribed form, that one named herein as *P. undosus*. With additional material I now realize that the Radwin and D'Attilio shell is the same as the Albany specimens of *P. undosus* and not *P. triformis*.

At the same time (Vokes, 1989, p. 5, text-fig. 7) I discussed a specimen from the Plio-Pleistocene Roe Calcarenite of southern Australia, suggesting that in this warmer water fauna both *P. triformis* and *P. acanthopterus* were found. However, with additional material of *P. undosus*, it is obvious that the specimen I called *P. acanthopterus* is a somewhat battered example of *P. undosus*, as it has a single large intervarical node between each pair of varices, in contrast to the two or three small nodes typical of specimens of *P. acanthopterus*.

This new species occurs together with *P. triformis* at Esperance, as is discussed above under that species. It is abundant throughout the harbor at Albany, and has been taken from numerous localities all around the southwestern corner of the continent. In general, specimens from the southern coast are smaller and not as elaborately flanged as those from Cape Naturaliste to Perth (compare pl. 6, figs. 1, 2, and figs. 3, 4).

As noted above, under *P. akation*, this new species is characterized by the pronounced undulation of the varical flanges, which also have strongly recurved projections marking the major spiral cords. From *P. akation* it differs in having a less massive shell, which attains a somewhat larger size (maximum length 60 mm), with a rounded shoulder. The varical faces are not as elaborately fimbriated as in *P. acanthopterus*, *P. triformis*, and *P. akation*, but resemble the smoother *P. duffusi*. From the latter, *P. undosus* differs in its larger size, less extended shoulder spine, and more expanded varices. As discussed above under Materials and Methods, the protoconch of *P. duffusi* is half again as large as that of *P. undosus* (diameter 1.5 mm vs. 1.0 mm).

ACKNOWLEDGEMENTS

My deepest gratitude goes to Joe Rinkens, Port Hedland, W.A., for his generosity in allowing me to select the best specimens from his collection of *P. acanthopterus* and *P. akation*, n. sp., to be studied. His insight into the ecologic requirements of the two forms was most helpful in my determination of the validity of the new species. To a number of Western Australian divers/shell collectors, I owe a tremendous debt for material to study and for information on ecology and geographic range. These include: Alan F. Longbottom, Grass Patch; Andrew Edinger, Esperance; Johan Pas, Albany; Steven J. Marshall, Augusta; Peter Ignoti, Witchcliffe; and John N. Campton, Trevor Sutcliffe, A.J. (Tony) Gabelish, and Hugh Morrison, all of Perth. I am also indebted to the entire staff of the Malacology Section of the Australian Museum, Sydney, but especially Winston F. Ponder and Ian Loch, as well as Fred E. Wells and Shirley Slack-Smith, of the Western Australian Museum, Perth, for the loan of specimens and for the hospitality extended to me while at their respective institutions. Henry W. Chaney, Santa Barbara Museum of Natural History, allowed me to borrow and "clean-up" the type specimen of *P. phillipsi* (in fact, assisting in the removal of the large colony of bryozoans adorning the dorsal side). Kathie Way, of the Mollusca Section, British Museum (Nat. Hist.) kindly sent to me the holotype of *Murex saibaiensis*, as well as Watson's example of *P. acanthopterus* from the Torres Strait, for study. Kevin Lamprell, Kallangur (Brisbane), provided specimens of *P. acanthopterus* from the Gulf of Carpentaria and the Torres Strait, as well as information of the dredgings there. He

also originally collected the preserved egg-capsule material held in the collections of the Australian Museum studied for text-figure 1. Zuzana Hruska, Coordinated Instrumentation Facility, Tulane University, made the SEM photographs of the radula in text-figure 3 and Marianna Kunow provided the art work for text-figure 1.

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